An enriched prey diet increases survival and growth rate in the early instars of two mantises

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Abstract

Within ecosystems, heterotrophs are limited by food availability and quality. Likewise, predator fitness is influenced by prey health and nutrition: Unhealthy prey can sicken their predators either through disease or nutritional inadequacy, while healthy prey can hasten predator development and enhance fecundity. Traditionally, studies on the effects of prey nutrition on predator fitness have been biased toward the larger stages, where prey-size limitations are less. However, insect fitness is affected by nutrition during all life stages. This study assessed the effect of flies fed either a standard diet (one that allowed for completion of the prey life cycle) or an enriched diet (higher in proteins, fats, and fiber) on early instar performance measures in two mantis species from different families. In both species, early development time was shorter by up to 2 days in the groups feeding on diet-enriched prey, and survival to the third instar was marginally higher. In *Creobroter apicalis* (Saussure, 1869) (Mantodea: Hymenopodidae), survival to the second instar was significantly higher in nymphs fed *Drosophila hydei* (Sturtevant, 1921) (Diptera: Drosophilidae) that had received an enriched diet, and the first and second instar durations were significantly shorter. Meanwhile, in *Tenodera sinensis* (Saussure, 1871) (Mantodea: Mantidae), neither survival to the second instar nor second instar duration were significantly affected by prey diet. These results show that prey feeding on a more nutritious diet (one higher in proteins and fats) can improve predator growth and survival rates but that different species have different responses to these factors.

Keywords

nutritional ecology, predation

Introduction

Predators are impacted by prey availability and prey health. Prey diet has profound impacts on predator growth rate, survival, and fecundity. For example, Wilder et al. (2010) fed adult females *Rabidosa rabida* (Walckenaer, 1837) (Araneae: Lycosidae) spiders starved or well fed (with dog food) *Acheta domesticus* (Linnaeus, 1758) (Orthoptera: Gryllidae) crickets and found that the spiders that ate the well-fed crickets extracted 15% more available lipids than those fed starved crickets. Similarly, Strohmeyer et al. (1998) found *Podisus maculiventris* (Say, 1832) (Hemiptera: Pentatomidae) reared on caterpillars fed higher protein diets to be 2% to 5% heavier at adulthood than those reared on caterpillars fed lower protein diets. Likewise, *Orius majusculus* (Reuter, 1879) (Hemiptera: Anthocoridae) reared on *Drosophila melanogaster* (Diptera: Drosophilidae) fed a diet supplemented with casein had 6% lower mortality and more eggs (5%) than those reared on *D. melanogaster* fed a diet supplemented with sucrose (Montoro et al. 2021). Finally, Mayntz et al. (2003) found that *Zygiella x-notata* (Clerck, 1757) fed *D. melanogaster* reared on a medium of 45% dog food had a 19% higher survival and 33% more rapid development (Araneae: Araneidae) than those fed *D. melanogaster* reared on a control diet.

There is limited research on the effects of prey quality on mantis fitness, with the available research focusing on adult mantids. For example, females of the mantids *Tenodera sinensis* and *Stagmomantis limbata* (Hahn, 1835) fed to satiation were found to be significantly less likely to consume their mates than females fed fewer or smaller prey items (Maxwell et al. 2010a, Maxwell et al. 2010b). In addition, females of *S. limbata* fed multiple prey species were found to live longer and have higher fecundity than females fed only one prey species (Maxwell et al. 2010b, Maxwell and Frinchaboy 2014).

Mantises present a unique opportunity to study the effects of prey nutrition on the early life stages of generalist predators, as they represent a trophic guild that is ubiquitous and has demonstrable effects on ecosystem functioning (Hurd et al. 2015, Korichi et al. 2016). While a study was conducted on dietary variety in late-instar nymphs of the mantid *Pseudomantis albofimbriata* (Stål, 1860) (Barry 2013), little is known about the effects of prey nutrition on early-instar mantises. In roaches, a closely related order of insects, early nutrition has been shown to affect adult fecundity. Early-instar females of the roach *Nauphoeta cinerea* (Olivier, 1789) fed a single-source diet produced fewer offspring than similarly aged females fed a multi-source diet, although both groups consumed the same multi-source diet in adulthood (Barrett et al. 2009). In

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mantises, *T. sinensis* nymphs that fed upon pollen in the first instar grew faster and were more likely to survive than nymphs that did not feed upon pollen (Beckman and Hurd 2003). The earliest stages of mantis development are the most vulnerable to mortality (Roberts 1937, Beckman and Hurd 2003), and thus the early performance of such predators can dictate their role in food webs at later stages of the life cycle. By understanding what factors limit the abundance of this trophic level, we can gain insight into the forces that dictate the interactions between organisms in ecosystems.

The small size of hatchling mantises should substantially limit their range of possible prey, which means that the number of prey species accessible to this life cycle stage should be smaller. As a result, it is expected that any given meal should have a greater effect on the insect's development than any given meal at later instars. This is because earlier instar nymphs are satiated on fewer prey items than later ones. Here, I present the results of an experiment in which I reared young nymphs of two mantis species on prey that had eaten a standard food source before being consumed by the mantises and compared the performance of the nymphs (early instar duration and survival) with that of nymphs reared on prey that had eaten an enriched food source before being consumed. This is a plausible ecological scenario wherein adult flies are either unable to access a nutritionally complete food resource before becoming prey or are encountered by the predator before they access such food. Various factors, such as habitat richness or the presence of competitors (invasive or native), can influence the food encountered by prey.

Materials and methods

Creobroter apicalis, initially obtained from an undisclosed European breeder and sent to Adrian Kleffner (mountainmantids) in Colorado were reared in 940 mL polypropylene cups with cloth-ventilated lids within a 120×60×150 cm mylar grow tent at 24+5°C, 55% RH, with a 16:8 L:D cycle. Lighting was provided with daylight-colored LED bars. The lids of the cups received cotton padding and were misted with deionized (DI)water every 2 days. Mated females were provided with plastic plants to oviposit upon. Oothecae from mated females were transferred to 940 mL polypropylene containers and hot-glued to the lid with the same misting regime as the adults. Within the incubation cup, a paper towel and shredded aspen were provided so hatchlings could perch. Containers were rinsed with hot water every 3 weeks, and cotton pads were replaced with the same frequency.

Oothecae of *Tenodera sinensis* were purchased from Mantisplace (Olmsted Township, OH) and eBay seller "crittergrr" (Bradenville, PA). Upon receipt, oothecae were hot glued to the lid of a container like those used to hold *C. apicalis* and refrigerated at 2°C until the experiments on *C. apicalis* were completed; this was done to satisfy the diapause requirement of *T. sinensis* eggs and to delay hatching for practical purposes. Refrigerated oothecae were misted with DI water weekly to avoid excessive desiccation. Once removed from the refrigerator, the oothecae and subsequent nymphs were kept under the same photic, thermal, and misting regime as *C. apicalis*.

Cultures of *Drosophila hydei* (Sturtevant, 1921) (hereafter, fruit flies) were maintained in a separate grow tent under the same internal conditions as the mantises. Cultures were made in 710 mL polypropylene containers with cloth-ventilated lids. The culture medium was made with Repashy Superfly (Repashy ventures, Oceanside, CA), a medium derived from yeasts, seaweeds, and fruits. Repashy superfly was prepared as instructed with one exception: to suppress flour mite (*Acarus siro*) outbreaks, 20% of the liquid volume added to the powder was white vinegar. Other measures to reduce *A. siro* densities included placing each culture in individual paper bowls containing approximately 2 cm of diatomaceous earth and the use of fruit flies from the first generation of culturing to seed new cultures. A single coffee filter and shredded aspen were stuffed within the fresh medium to allow the fruit flies to cling to perches above the medium. Three days later, about 20 mature fruit flies were added. New cultures were created each month.

Pangea apricot crested gecko diet (CGD) was chosen as a rotting fruit simulant. This CGD was formulated by scientists (Donoghue and McKeown 1999) to mimic rotting fruits and plant matter that would be encountered by various detritivore species. The CGD contains fruits, fungal extracts, and insect proteins, which represents a realistic ecological food resource. In nature, rotting fruits tend to be teeming with various decomposers across taxa, and their associated proteins and other materials would be expected to be present throughout the rotting matter.

To make the enriched diet available to the fruit flies, 2 g CGD was smeared along the inner walls of a 940 mL polypropylene cup with a cloth-ventilated lid. Then, approximately 100 fruit flies were placed into the cup. Fruit flies were maintained in the grow tent with the nymphs like this for 12 h (which represents approximately 7% of the fruit fly's adult lifespan) before 2 fruit flies were added to each gut-load nymph cup (4 for *T. sinensis*). Subsequently, the control group larvae received 2 fruit flies each (4 for *T. sinensis*) directly from the cultures (i.e., no fruit flies were starved). During the experiment, most of the nymph cups had uneaten fruit flies in them, indicating that the nymphs had been fed to satiation.

Upon hatching, the nymphs were misted with DI water and split into individual containers. *Creobroter apicalis* hatchlings were transferred to 118 mL polypropylene portion cups, while *T. sinensis* nymphs, which are nearly 4 times the length of *C. apicalis* at hatching, were transferred to 473 mL polypropylene cups. Cups for *C. apicalis* were modified in the following ways: A paper towel sliver approximately 2 cm wide was hot glued up one side of the cup to absorb moisture for humidity maintenance and to allow the nymph to climb around the cup, and a 3 cm wide hole was soldered into the center of the lid and covered with a sheet of mesh hot glued over the hole. Moist cotton pads were placed over such holes. Cups for *T. sinensis* were modified with a similarly sized paper towel sliver running up the sides, but a cloth-ventilated lid and a full cotton pad covered these cups for airflow and humidity control. For both species, the cups were placed randomly on shelves and randomly reshuffled to avoid pseudoreplication. For *C. apicalis*, 45 nymphs per group (90 total) from 2 separate hatchings were used. For *T. sinensis*, 60 nymphs per group (120 total) from 1 hatching were used.

Nymphs in each group of *C. apicalis* were offered 2 fruit flies every other day during both the first and the second instars. Nymphs in each group of *T. sinensis* were offered 4 fruit flies every other day during the first instar and 6 fruit flies every other day during the second instar. These numbers of prey were decided on by observing nymphs in previous iterations of rearing feeding to satiety in early instars.

The performance measures of survival and development rate (number of days in the first and second instars) were recorded for each nymph. Due to practical (financial and space) constraints on rearing large numbers of older nymphs/adults, the experiment was run only for the durations of the most vulnerable early instars of these insects. To rule out the effect of sex on performance measures (*C. apicalis* females are larger than males and have an extra instar), nymphs of both species were sexed at the third instar to determine the sex ratio of each treatment group. Two-sided t-tests were run

on the durations of the first and second instars of nymphs by treatment. G-tests of independence were performed on the proportions of surviving nymphs per treatment (fly diet) group. To ensure that there was no sex-biased survival in either treatment group, as has been seen in other studies on insect nutrition proportion tests on the number of females by treatment were run. Separate analyses were run by species. All data were analyzed using R (version 4.0.3).

Results

Creobroter apicalis.—Survival to the second instar between the control and diet-enriched groups was 87% and 100% (Fig. 1), respectively, with the diet-enriched nymphs having significantly higher survival to the second instar (G = 8.75, df = 1, p = 0.003). Nymphs in the control group spent an average of 17.4+3.1 (SD) days in the first instar, while nymphs in the diet-enriched fly group spent an average of 16.2+1.9 (SD) days in the first instar (Fig. 2, t = 2.0, df = 60.6, p = 0.05). Cumulative survival to the third instar (Fig. 1) in the control group was 80%, which was marginally significantly different (G = 3.602, df = 1, p = 0.058) from 96% in the diet-enriched group. The nymphs in the control group spent an average of 14.3+3.07 (SD) days in the second instar, while those in the diet-enriched group spent an average of 12.7+1.74 (SD) days in the second instar (Fig. 2, t = 2.71, df = 53.5, p = 0.01). Average total time to third instar in the control group was 32.0+3.3 (SD) days, while that of the diet-enriched group was 29.0+2.1 (SD) days. This difference was significant (t = 4.4, df = 58.1, p = 5.2×10^{-5}). The male:female ratio of the control group was 0.41, while that of the diet-enriched group was 0.46 (x^2 = 0.025, df = 1, p = 0.87).

Tenodera sinensis.—Survival to the second instar between the control and diet-enriched groups was 100% and 95% (Fig. 3), respectively, with no significant difference in survival between treatment groups (G = 3.602, df = 1, p = 0.058). Nymphs in the control group spent an average of 12.3+0.9 (SD) days in the first instar, which was significantly longer (Fig. 4, t = 3.61, df = 109.64, p < 0.0005) than the 11.8+0.7 (SD) days spent in the first instar by the diet-enriched group. Cumulative survival to the third instar (Fig. 3) in the control group was 53%, which was marginally significantly different (G = 2.88, df = 1, p = 0.09) from 68% in the diet-enriched group. The nymphs in the control group spent an average of 15.8+2.7 (SD) days in the second instar, while those in the diet-enriched group spent an average of 15+2.2 (SD) days in the second instar (Fig. 4, t = 1.44, df = 57.1 p = 0.16). The average total time to third instar in the control group was 28.0+2.4 (SD) days, while that of the diet-enriched group was 25.4+9.4 (SD) days. This difference was only marginally significant (t = 1.7, df = 46.9, p = 0.1). The M:F ratio of the control group was 0.48, while that of the diet-enriched group was 0.47 ($x^2 = 7.3*10^{-31}$, df = 1, p = 1).

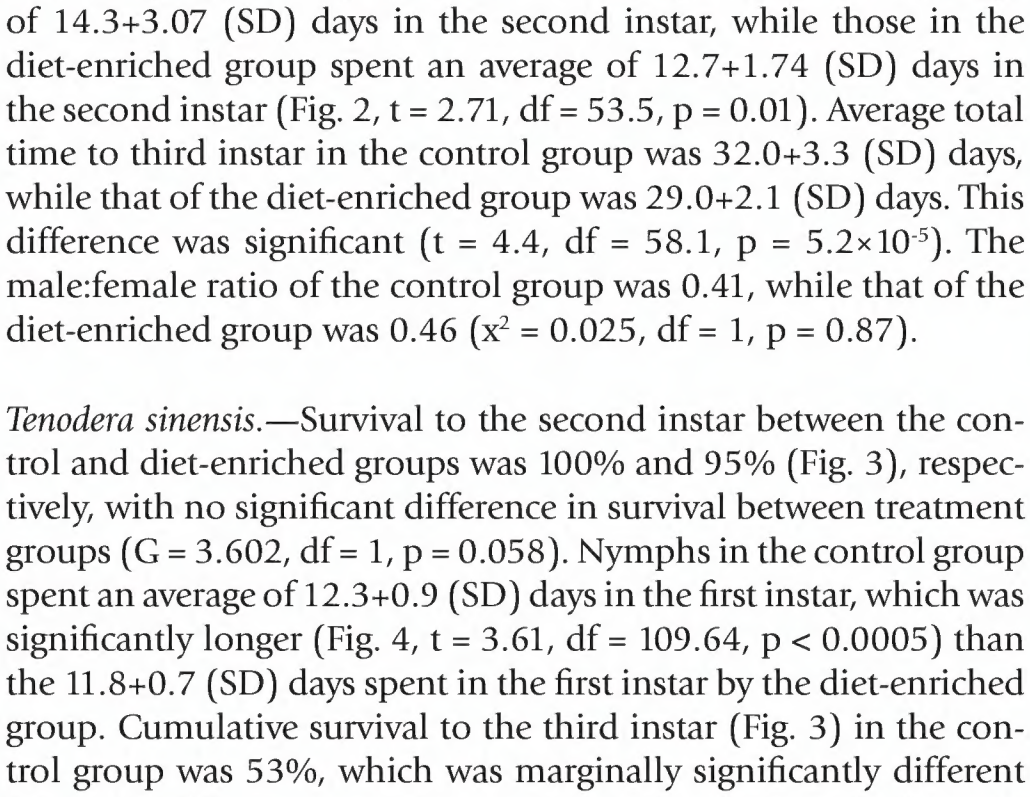

Fig. 1. Percent survival to second instar (top) and percent survival to third instar (bottom) for *Creobroter apicalis*.

Discussion

The mantis nymphs tended to perform better when their prey had consumed an enriched diet. While survival to the second instar in *T. sinensis* did not vary significantly by treatment, survival to the second instar in *C. apicalis* did. Survival to the third instar was also higher in both species given varied-diet-fed prey. Since the first 2–3 instars in mantises account for up to 90% of mortality throughout the life cycle (Roberts 1937), it is probable that nymphs surviving to the third instar would survive all the way to maturity. In both species, first instar duration was shorter (by almost 3 days in *C. apicalis* and 1.5 days in *T. sinensis*) when prey had an enriched diet. While the differences were only by a few days, protracted through the 6 or 7 instars of these mantises, maturation may be accomplished a week or more earlier. This is especially important for the temperate *T. sinensis*, as it needs to complete its life cycle before it is killed off by fall frosts. More rapid development may also be associated with passing through vulnerable early instars more quickly and a quickening of the ability to consume a greater diet breadth, which is positively correlated with improved performance in other predatory species (Maxwell et al. 2010b, Dudova et al. 2019).

Creobroter apicalis was found to be more susceptible to differences in prey diet quality than *T. sinensis*. The survival to and duration of the second instar in *C. apicalis* differed significantly between treatment groups, while neither metric varied significantly for *T. sinensis*. *Tenodera sinensis* is the world's second most widespread mantis, having invaded much of the temperate world except for Antarctica (Crowder and Snyder 2010). Thus, it may have better compensatory mechanisms to cope with nutritional deficits, or it may be more

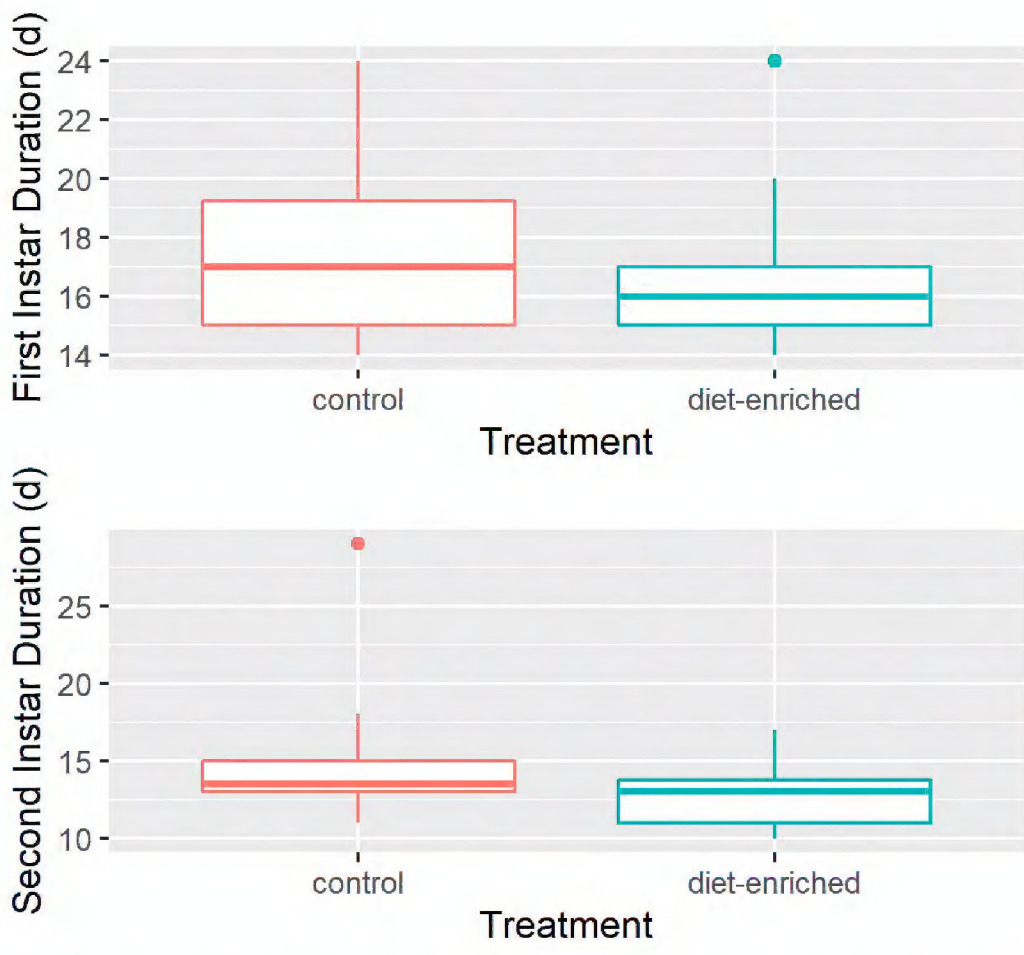

Fig. 2. Time (in days) to second instar (top) and time (in days) to third instar (bottom) for *Creobroter apicalis*.

efficient at converting prey biomass to its own biomass. While no relative growth rate measurements were taken, it should be noted that *T. sinensis* nymphs are about 4 times the size of *C. apicalis* nymphs at the same instar. Despite the need for this species to add more biomass per instar, it still managed to pass through its instars more rapidly. Therefore, I postulate that (from a caloric perspective) the prey-predator biomass conversion of *T. sinensis* is more efficient, at least under our experimental conditions, than that of *C. apicalis*.

While protein in the diets of prey may account for these differences, it should be noted that the diets fed to the flies had other differences as well. For example, the fruit fly medium fed to the control group's prey had a fat content of 0.8%, while the food fed to the diet-enriched group's prey had a fat content of 4.7%.

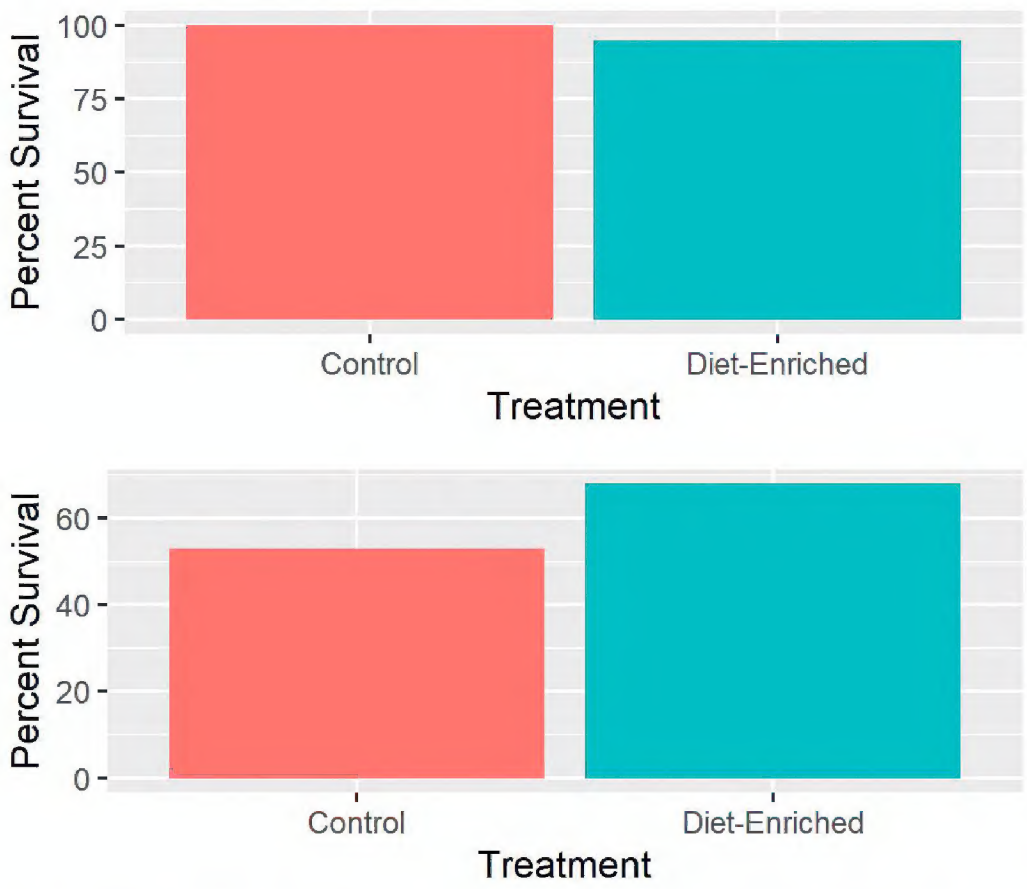

Fig. 3. Percent survival to second instar (top) and percent survival to third instar (bottom) for *Tenodera sinensis*.

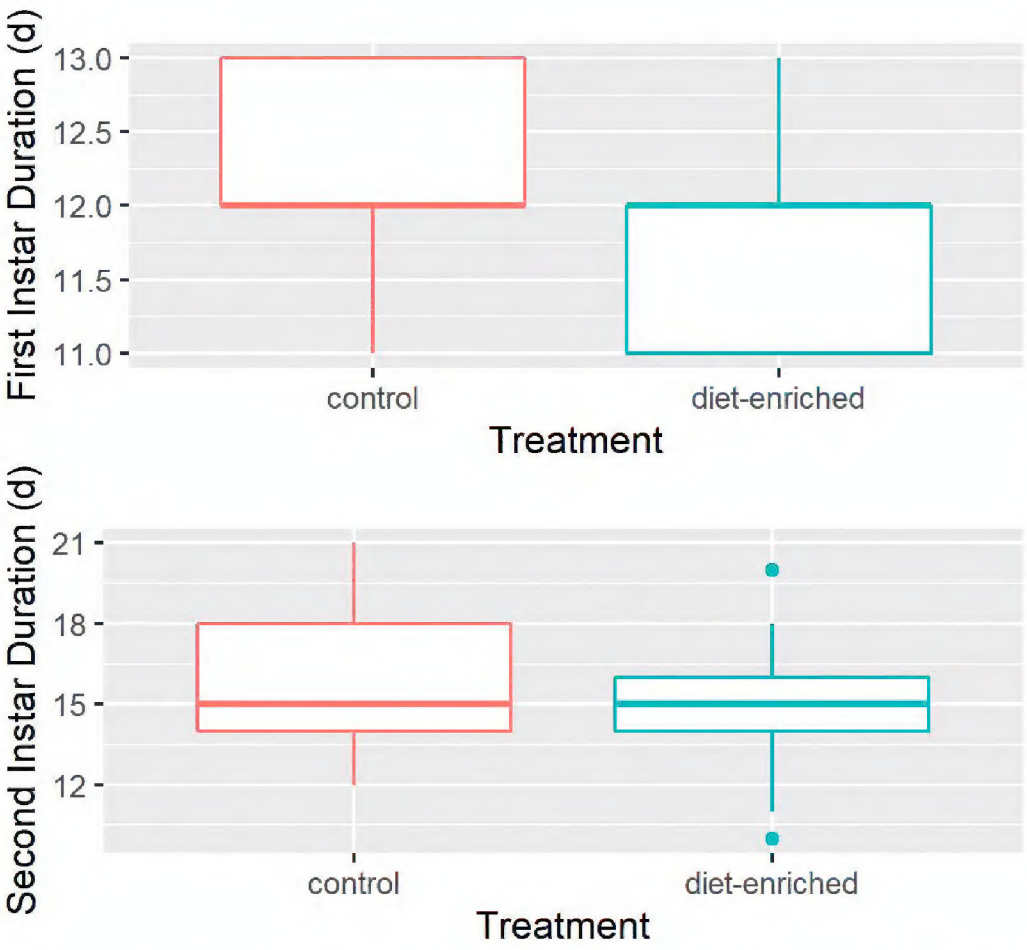

Fig. 4. Time (in days) to second instar (top) and time (in days) to third instar (bottom) for *Tenodera sinensis*.

Meanwhile, the fiber of the control group's prey's diet was 2%, while that of the diet-enriched group's prey was 8%. In spiders, the protein content of prey diet has been shown to not make a significant difference in the predators' performance measures, although lipid content does (Wilder et al. 2010, Koemel et al. 2019). The fruit flies fed an enriched diet may have had a more complete nutritional profile than the ones fed the control diet.

More study is required in this area. I do not know the underlying mechanisms for why the performance measures of these two mantis species were not parallel. More than likely, there are differences in how these species metabolize their food, and this may indicate differences in life-cycle strategies. *Creobroter apicalis* adult females live 5–6 months after their final molt and can deposit upwards of 12 oothecae throughout their lifespans, each containing between 50 and 90 eggs. Meanwhile, *T. sinensis* females survive a comparable length of time but instead deposit 1 or 2 oothecae during their lifespans, each containing 250 or more eggs. It is possible that biomass allocation essential to reproduction occurs at different ontogenetic stages between these 2 species. It is also possible that the thermal optima for the digestive enzymes of the tropical *C. apicalis* are narrower than those for the temperate *T. sinensis*. *Tenodera sinensis* is found to persist only in regions where seasonal degree-day accumulation is between 3200 and 4000 (Rooney et al. 1996) *C. apicalis*. Meanwhile, *C. apicalis* is only known from tropical Asia: India east to Vietnam (Yadav et al. 2018). There is little literature on the preferred habitat type of *C. apicalis*, and so a comparison to the habitat used by the more well-studied *T. sinensis* is not currently possible. However, different mantis taxa in the same location have shown differences in habitat and prey type usage (Rathet and Hurd 1983, Korichi et al. 2016), suggesting differences in prey usage by these two species. Tropical and temperate food webs may differ fundamentally, and therefore a consideration of how a consumer's food assimilation affects its dietary breadth is required. Because *T. sinensis* appears to be less affected by prey nutritional status than *C. apicalis*, it is very possible that this species has more plasticity in the food it is able to utilize. The choice of these species in the experiment reflects that they are both easy to obtain and easy to maintain in culture. However, additional species should be examined to obtain a clearer picture of how mantises respond to prey nutritional status.

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